

A PHYLOGENETIC MODEL FOR NORTH-EURASIATIC TUBIFLORAE ON THE BASE OF COMPARATIVE MORPHOLOGY, ZYTOGENETICS AND ECOLOGY*

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Many papers have been written about evolution and phylogeny of organisms. Very often missing informations have stimulated more or less probable hypotheses.

But extensive phylogenetic surveys of genera or even of families still are very seldom. That may derive from the fact, that especially in plant phyla fossil traditions over more extent geological periods are very rare; in other words, within higher plants they can be characterized as exceptions.

Therefore indirect methods are requested, and indeed they have been treated with success.

At first I think in the accurate classic morphological and anatomical analysis, in connection with zytogenetic investigations of recent species.

Zytogenetics comprises an extent evaluation of chromosome behaviour, like number and morphology or banding properties, respectively.

Last not least also the ecological adaptation of related species and their distribution patterns procure very important insights into the course of evolution.

One of the first most impressive classical analyses comes from Iren Manton (1934). She could demonstrate, that within the genus *Biscutella* (Brassicaceae on Cruciferae) diploid species ($2n=18$) could survive the Pleistocene period between the glaciation of Central and Northern Europe in favoured micro-refuges along the valleys of pleistocene streams. From there and shurely from other refuges in the North-Alps themselves younger tetraploid species ($2n=36$) have colonized the (inner formerly glaciated parts of the) Alps.

Darlington in Great Britain and Tischler in Germany, Navashin, Stebbing and others in America favoured those investigations, which brought out i.e. the

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very comprehensive analysis of the Cichoriaceae genus *Crepis* by Babcock (1947).

Later in Austria Enrendorfer favoured the examples of Babcock and Stebins in Europe. Ehrendorfer (1958) presented a very good example of the evolution of the subgenus *Leptogallium* of the *Gallium* (Rubiaceae). He took into his considerations also the influence of the Pleistocene period, and he tried to reconstruct the probable phylogenetic evolution of the *Gallium anisophyllum* complex in the European Mountain regions.

One has to consider, that the recent areas of diploid ($2n=22$) and tetraploid taxa ($2n=44$) are clearly disjunct, whilst now the diploids grow in areas with a minimal influence of Pleistocene glaciation, the tetraploids occupy the largest areas between the diploid and other higher polyploid species. Hexaploid ($2n=\pm 66$) and octoploid species ($2n=\pm 88$) have a closed distribution, they occur chiefly in formerly glaciated parts of the Alps and Pyrenees. A decaploid ($10x$) subspecies of *G. anisophyllum* solely occurs in the North Apennines.

Recently an other model has been derived from the genus *Pulmonaria* (Boraginaceae), also regarding the situation from the end of Pleistocene period up to now in northern Eurasia.

The area of the genus *Pulmonaria* extends from the Northwest of the

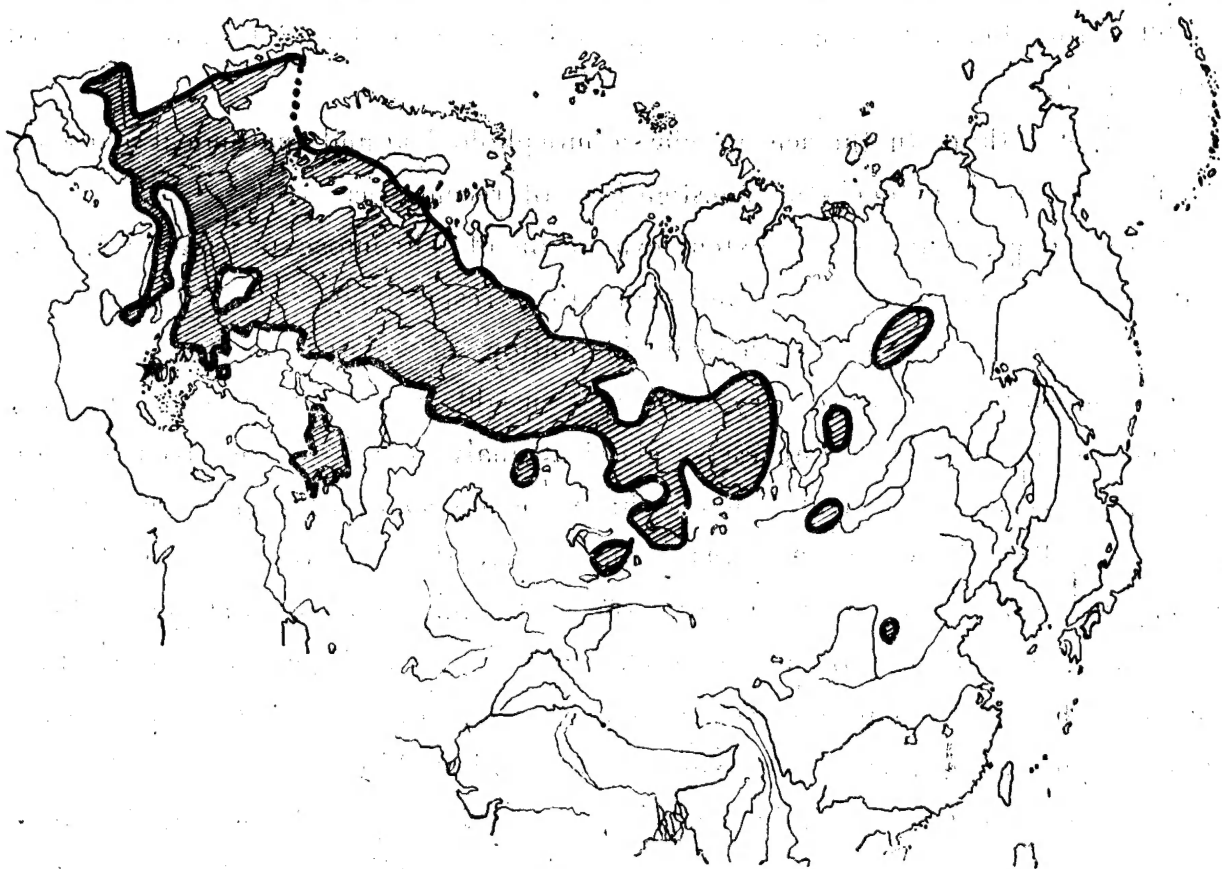


Fig. 1 Distribution of the genus *Pulmonaria* in Eurasia. ★ = genus *Paraskevia*, a small endemic genus of South Greece which is near related to the genus *Pulmonaria* (Original).

Iberian Peninsula to East-Siberia and North China, and from Britain and South Scandinavia, respectively to Central Greece (fig. 1).

Since Gams 1927 generally it has been accepted, that most of the recent species would have originated from 4 Tertiary species (groups) by extend and repeated interspecific hybridization. The Central European-Sarmatic *P. angustifolia*, the East Central European-East/Southeast *P. mollis*, the North Balkanic-Central European *P. officinalis*, the Carpathic-Balkan *P. rubra*.

New data obtained from many populations of nearly the whole habitat area of the genus pointed out, that there have taken place several strategies in the course of phylogenetic evolution of this genus, in which infraspecific hybridisation has taken place in a more different manner as Gams has suggested.

The small morphological differentiation of species in general suggests the assumption, that the recent *Pulmonarias* might represent a young group with a very small number of diacritic characters.

The predominantly ovate-lanceolate leaves (fig. 2) represent a series of

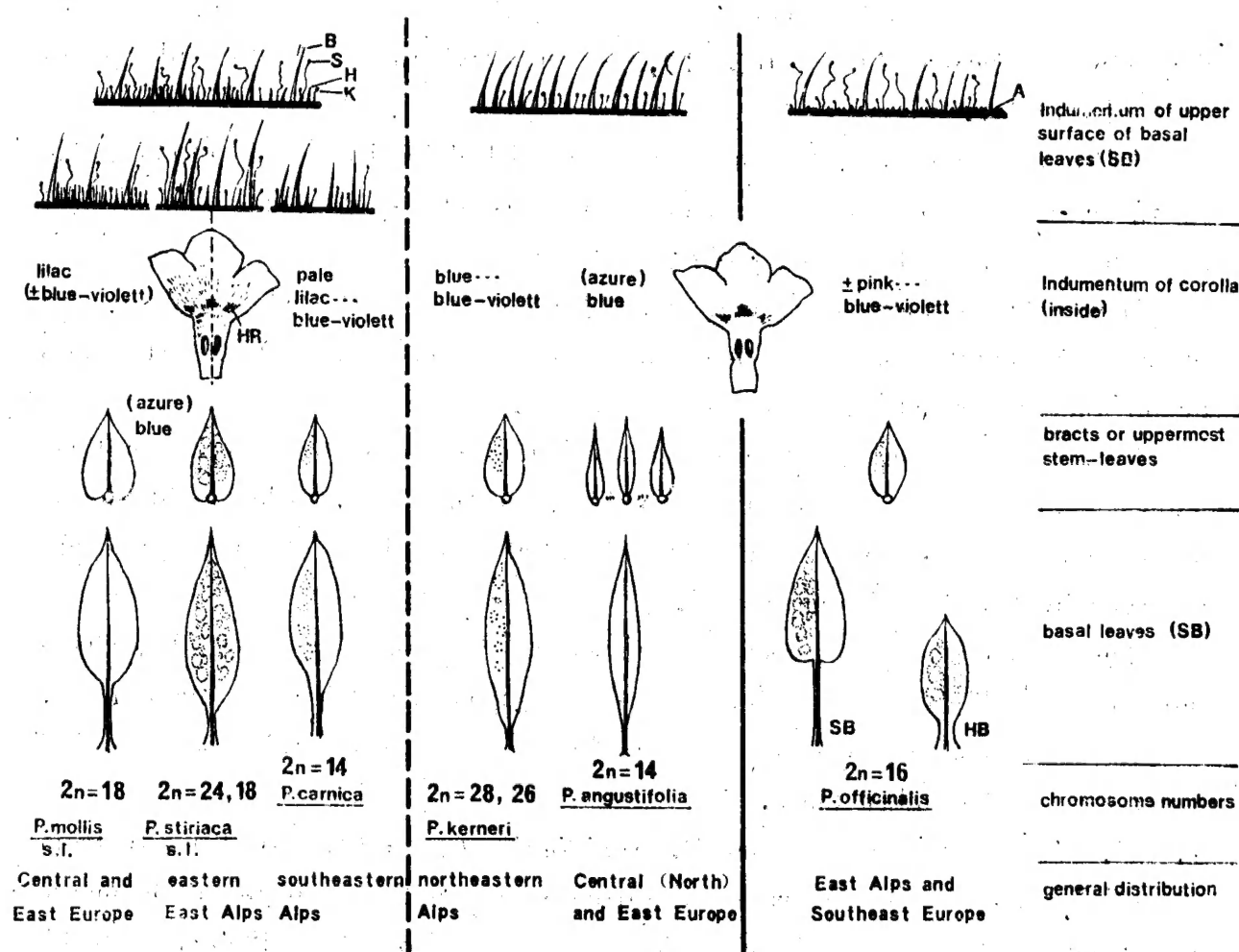


Fig. 2 Schema of the most important diacritic characters of the genus *Pulmonaria*. A = aculeoli, B = bristles, H = hairs, HB = late grown basal leaves ("autumn-leaves"), HR = circle of hairs at the border between limb and tube of corolla, K = very short glandular hairs, S = long stalked glandular hairs, SB = at first grown basal leaves ("summer-leaves"), (From Sauer 1976).

forms with very narrow to broad laminae and with a ground gradually tapering into the petiole or forming laminae with cordate or cuneate bases (mainly *P. obscura* and *P. officinalis*).

The main characters lie within the indumentum. According to the different groups (s. fig. 2):

1. only approximately equal long bristles (setae) may occur (i.e. *P. angustifolia*), or
2. only very unequal setae are composing the indument (*P. montana* group), or
3. long setae are mixed within a more or less dense indumentum of hairs and stalked glands (*P. mollis* group, *P. stiriaca*, *P. vallarsae*), or
4. only few long setae are scattered between numerous very short aculeoli (*P. officinalis*, *P. obscura*).

Also the inner surface of both the tube and limb of corolla are covered with a more or less dense indumentum of short silky hairs or they are smooth (this indumentum has not to be changed with the specific circle of hairs on the border between tube and limb (fig. 2), which is characteristic for all species of *Pulmonaria*).

At first Karyological data have been published by Tarnavski (1935). He found on the base of $x = 7$ diploids as well as tetraploids and still very bad understood "aneuploids" or dysploids, respectively.

New data obtained from many populations of nearly the whole habitat area of the genus pointed out, that there might have took place several strategies during the phylogenetic evolution of this genus.

Fig. 5 demonstrates the species groups (screened geometric figures) in their natural connection - arranged on the abscissa. On the ordinate the ploidy-levels are listed from the bottom up. The essential alterations of karyotypes are recorded by "marker chromosomes".

The common basic chromosome number of the genus is $x = 7$. The chromosomes of all species are either metacentric/submetacentric or subtelocentric.

In the course of evolution on the diploid level a considerable karyological differentiation has taken place.

1. *P. obscura* ($2n = 14$) and *P. officinalis* ($2n = 16$) differ clearly from other diploids by two pairs of chromosomes with 2 distal euchromatic segments. *P. officinalis* might have originated from the old "obscura stock" by doubling one chromosome pair on position III (s. fig. 3), so it got the new chromosome number $2n = 16$ ($2n = 14-16$). The other diploid *Pulmonarias* wear a single euchromatic segment, only at the distal end of

the longer arm. After Pleistocene this species might have spread from Balkan peninsula to Central Europe and north and south of the Alps (fig. 3).

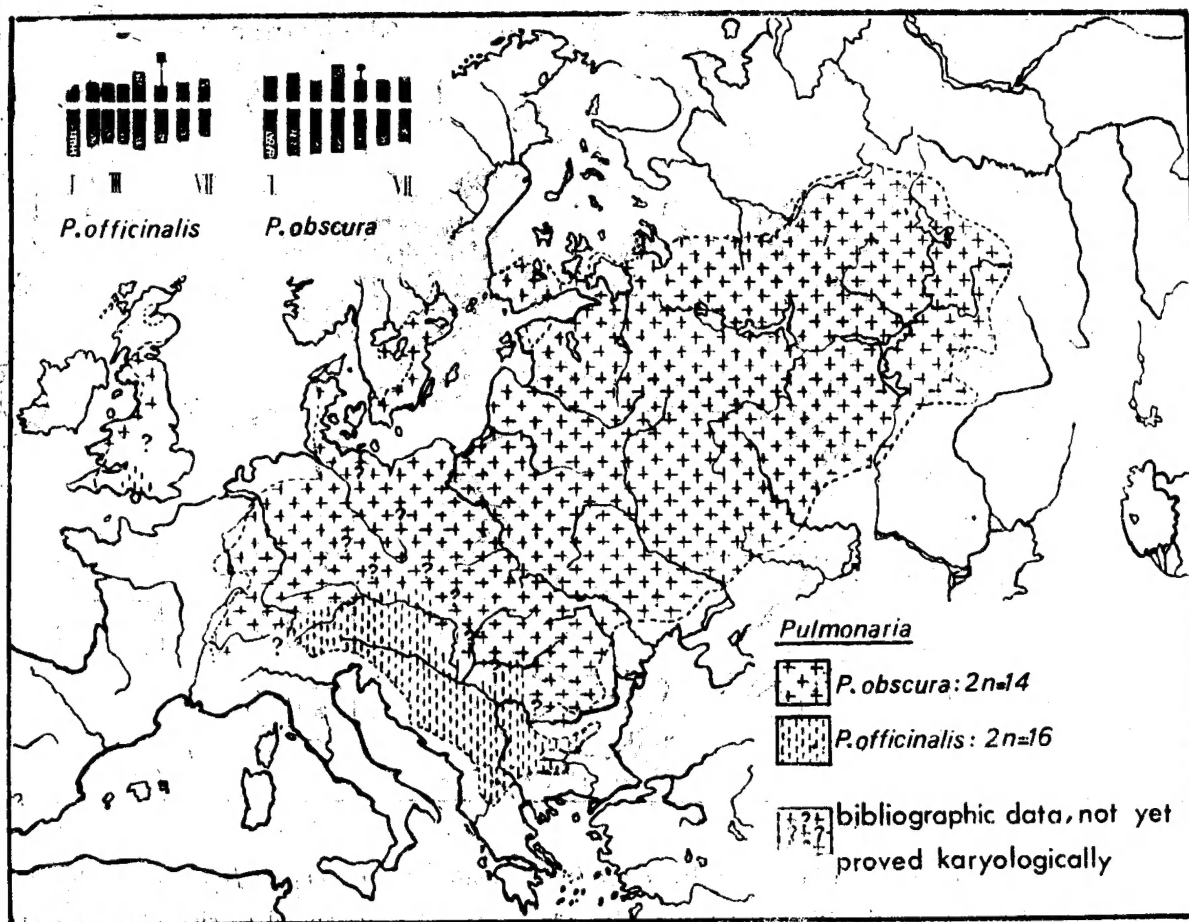


Fig. 3. Idiograms and distribution of *P. obscura* and *P. officinalis*. (According to Sauer 1975)

2. In the *P. angustifolia* group a clear separation into different karyotypes has occurred (fig. 4). The idiograms of species from eastern Central Europe ($2n = 14$) show primarily meta- or submetacentric chromosomes and satellites on the longest (subtelocentric) chromosomes of position I (fig. 4). These species may also represent a more primitive status.

The idiograms of species from western, southern, and southwestern boundaries of the area show a more advanced status. Their chromosomes are either subtelocentric or the idiograms are characterized by an increasing number of satellites or by clear "other" secondary constrictions on position III, IV, and V. Furthermore it is to be noted that the heterochromatic segments of the chromosomes have become longer.

The real *P. angustifolia* is characterized by a Central European-Sarmatic distribution (fig. 4). Relics, sometimes with an still uncertain taxonomic status and sometimes with tetraploid chromosome number ($2n=28$) have been found in

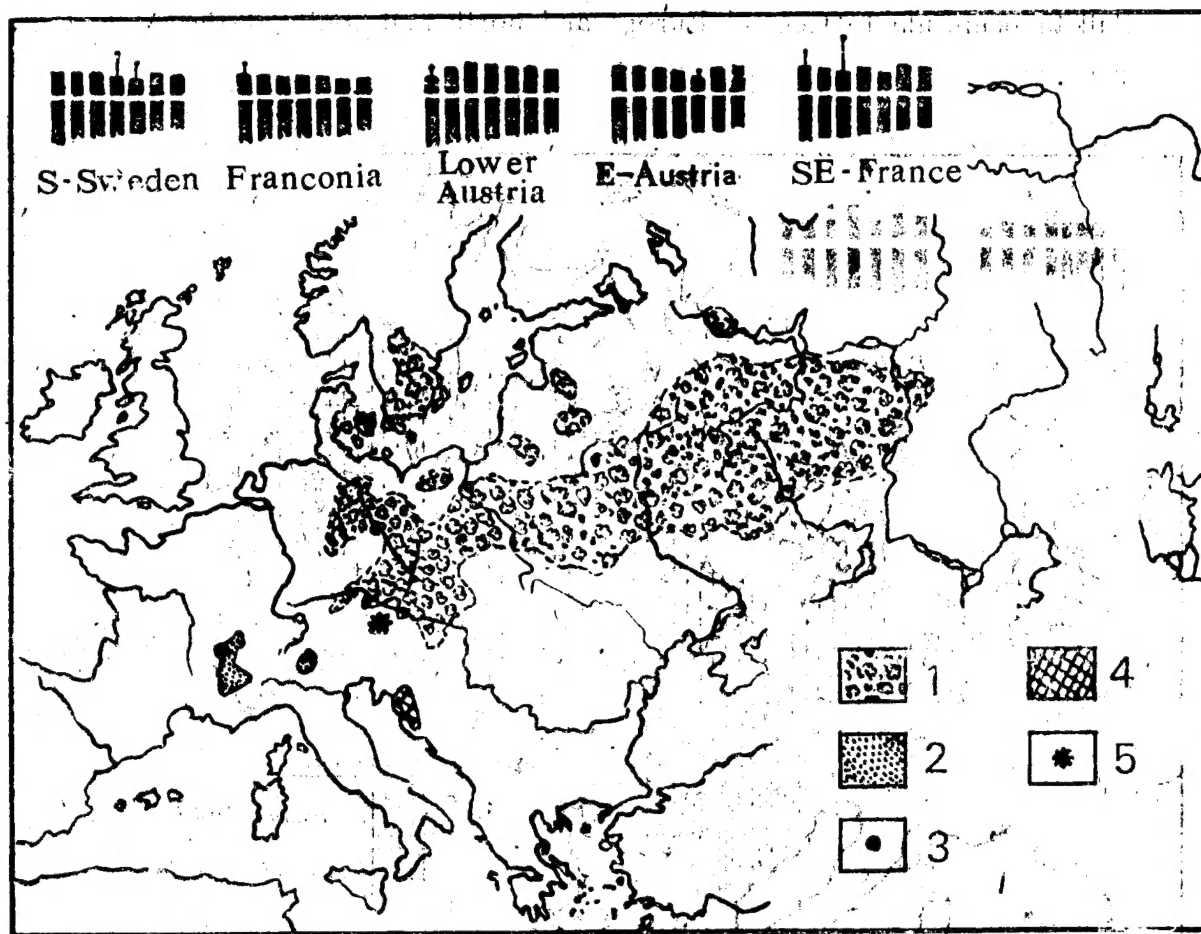


Fig. 4. Idiograms and distribution of *P. angustifolia* group. 1 = *P. angustifolia* s. str. ($2n=14$); 2 = *P. angustifolia* s. l. of the West and South Alps ($2n=14$); 3 = tetraploid species ($2n=28$); 4 = *P. visianii* ($2n=14$), endemic to Northwest Balkan Peninsula; 5 = *P. kernerii* ($2n=26, 28$), endemic to Northeast Alps. (According to Sauer 1975 and unpublished data).

the West Alps. Very near related to these species is the also diploid *P. visianii* ($2n=14$) of Northwest-Yugoslavia.

3. The next two groups are characterized by metacentric and subtelocentric chromosomes. The chromosomes of *P. dacica* ($2n=14, 28$) and *P. filarszkyana* ($2n=14$) are marked by very long heterochromatic segments. The idiograms indicate a close relationship on the one hand between *P. dacica* and *P. filarszkyana* as well as between *P. rubra* and *P. carnica* (both $2n=14$) on the other hand. These species may be interpreted as relic species of a diploid complex with a formerly wider distribution. To these species have to be joint the dysploid groups of *P. mollis/collina* ($2n=18$), *P. australis* ($2n=20$), *P. stiriaca* ($2n=18, 34$), perhaps, also *P. vällar-sae* ($2n=22$). They are centered in East Southeast and South-Europe (fig. 5, 6).

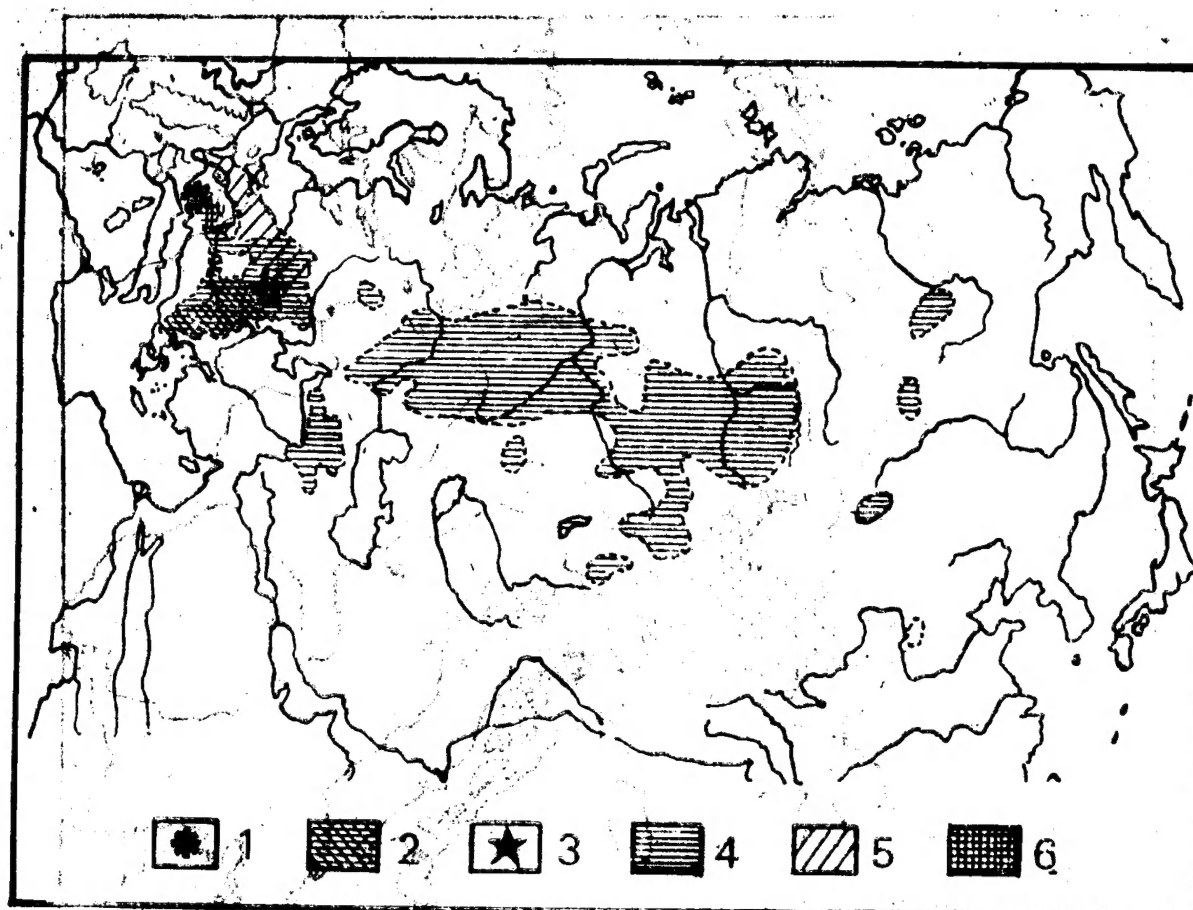


Fig. 5 Distribution of euploid and dysploid East European and Asiatic *Pulmonaria* species. 1 = *P. carnica* ($2n=14$), endemic to Southeast Alps; 2 = *P. rubra* ($2n=14$), Carpathian Mountains, East and Central Balkan Peninsula; 3 = *P. filarszkyana* ($2n=14$), endemic to north Carpathian Mountains; 4 = *P. dacica* s. l. ($2n=14, 28$); 5 = *P. mollis* and *P. collina* ($2n=18$); 6 = *P. stiriaca* ($2n=18, 24$), border of East Alps. (According to Sauer 1975 and unpublished data)

New evidences point out, that the dysploid derivatives of these groups might have evolved in the periglacial parts of Southeast and South Europe from a diploid stock of ancestors with $n=7$ or $2n=14$ (fig. 7). The just found deviating chromosome numbers $2n=20$ and $2n=22$ might have originated from still unknown triploids of the Central Balkan peninsula. There also intraspecific hybridization might have lead to species with $2n=18$ (*P. mollis* group). Obviously the combination of unreduced gametes of diploids ($n=14$) with reduced gametes of hypotriploids ($n=10$) might have given rise to the new chromosome number $2n=24$. Morphological evidences (cf. fig. 2) and distribution patterns (cf. fig. 5, 6) suggest, that these events might have happened parallelly in different groups.

4. The species of *P. longifolia* group are characterized by metacentric and subtelocentric chromosomes and also by satellites on the position II. The recent *P. saccharata* group and *P. montana* group do not possess diploids,

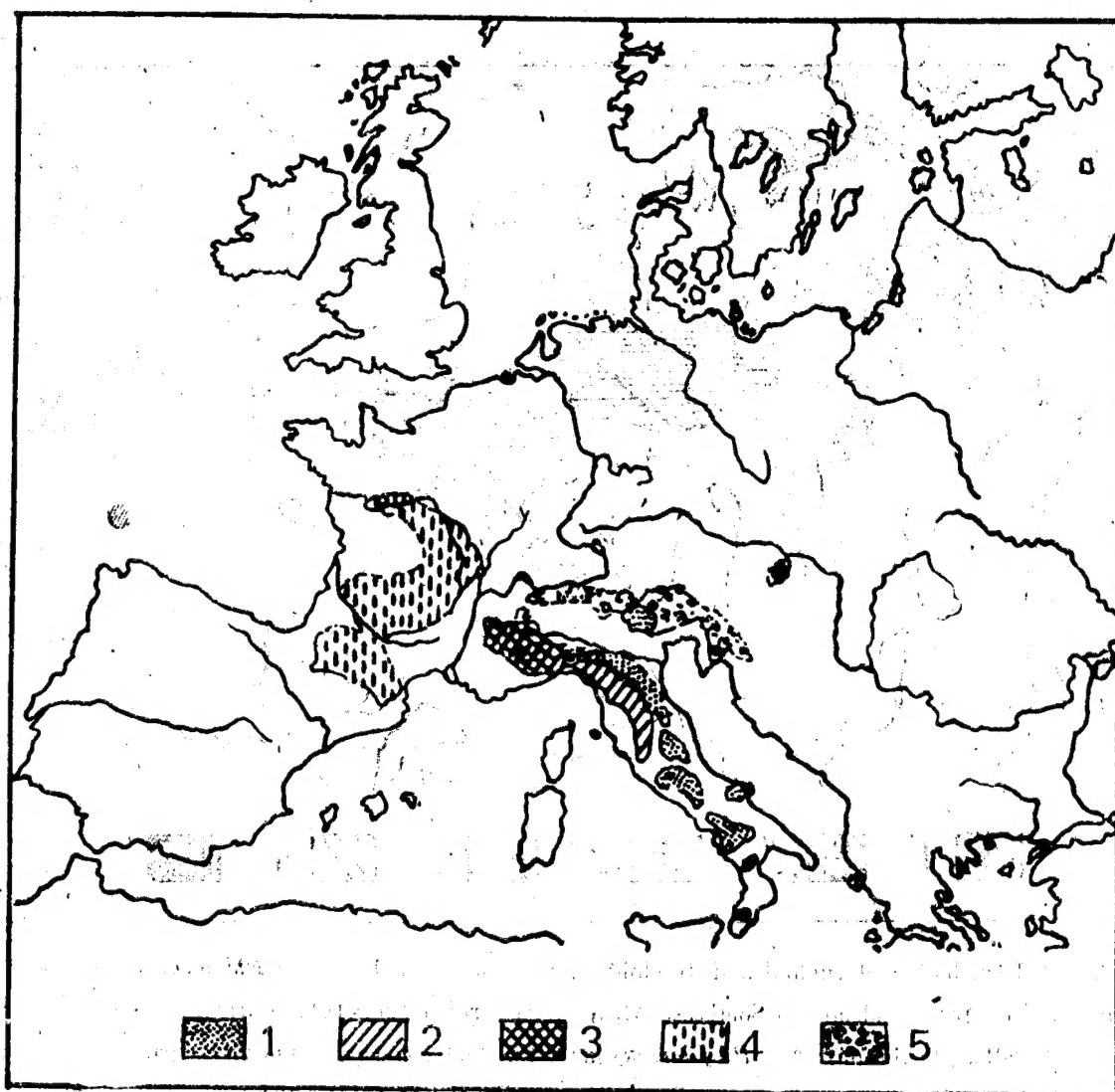


Fig. 6 Distribution of dysploid South European as well as of South and East and one West European *Pulmonaria* species. 1 = *P. vallisae* s. l. ($2n=22$), 2 = *P. saccharata* s. l. ($2n=22, 26, 28$), 3 = probable introgressive complex between *P. vallisae* s. l. and *P. saccharata* s. l. ($2n=22, 26$), 4 = *P. affinis* ($2n=22$), 5 = *P. australis* ($2n=20$). (According to Sauer 1975, Bolliger 1982)

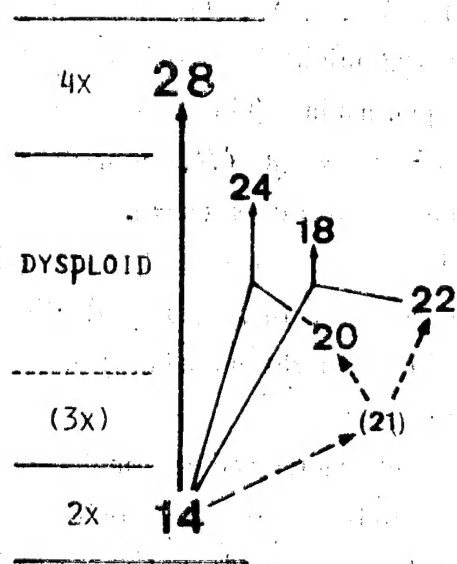


Fig. 7. Diagram representing the probable karyological evolution within Central and Southeast and South European traploid and dysploid *Pulmonaria* groups (*P. dacica*, *P. mollis*, *P. stiriaca*, *P. australis* pro pto, and probably *P. vallisae*) from a diploid stock of ancestors. For further explanation see the text. (Original)

The comparison of numerous idiograms signal, that they might have originated from different ancestors in the south or southwest of the Alps (fig. 6. 8).

The descend of *P. montana* from the *P. longifolia* branch already has been disclosed by karyotype analysis. Recently this state could be confirmed by Bolliger (1982). He pointed out, that the former *P. longifolia* group has been separated into four younger subspecies with very complicated karyological evolution by polyploidy (ortho- and anorthopolyploidy) and dysploidy (fig. 9). Intraspecific hybridisation and not reduced gametes might have played a decisive role within the evolution of *P. longifolia* group ($2n=14, 20, 22, 26, 28, 30, 38$), from which also the *P. montana* complex ($2n=22, 24, 26, 28$) might have originated also by a characteristic morphologic differentiation (cf. fig. 2, 8).

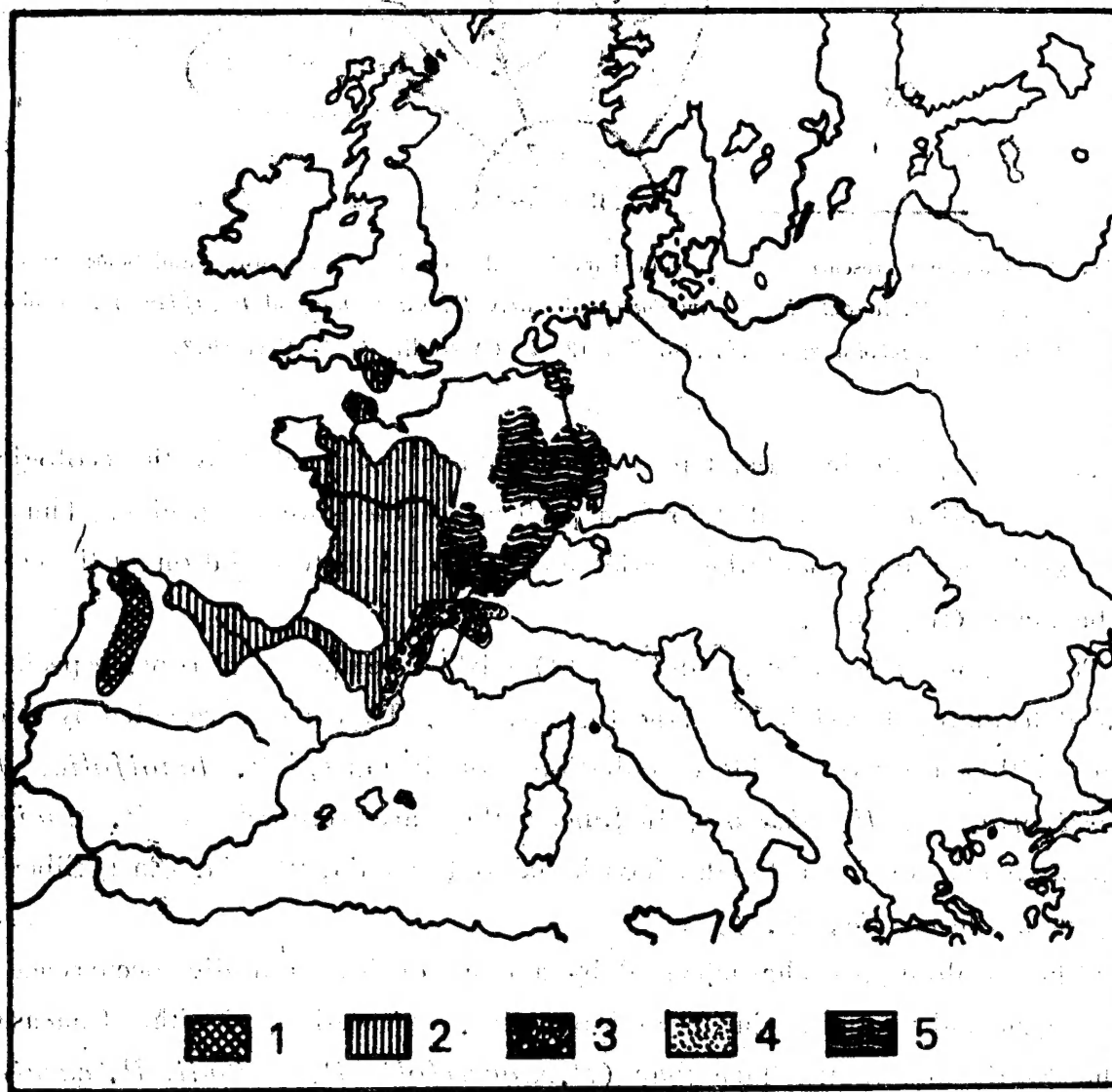


Fig. 8 Distribution of euploid and dysploid West and Southwest European *Pulmonaria* species. 1 = *P. longifolia* subsp. *glandulosa* ($2n=14$), 2 = subsp. *longifolia* ($2n=14, 20, 22$), 3 = subsp. *delphinensis* ($2n=20$), 4 = subsp. *cevenensis* ($2n=20$), 5 = *P. montana* ($2n=20, 22, 24$), (According to Sauer 1975, Bolliger 1982)

A similar course of evolution can be accepted also for the *P. saccharata/affinis* group, but the center of their evolution might have been situated more southward (s. fig. 9) .

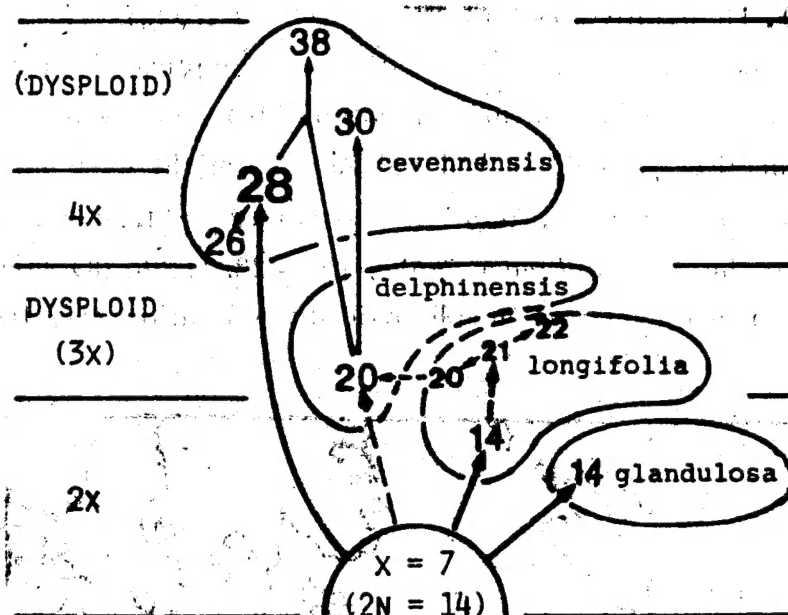


Fig. 9 Diagram representing the probable karyological evolution of Southwest and South European *Pulmonaria* groups (*P. longifolia*, *P. montana* and partly *P. saccharata* and *P. affinis*), explained by means of the *P. longifolia* group cf. also fig. 12) . (According to Bolliger 1982)

These morphological and karyological data are supported by the ecological features as well as by the distribution patterns of the known species. Thus a more exact statement about the spatial and temporal differentiation of the genus can be made (fig. 10) .

Today a broad belt of diploids ($2n=14$) exists in temperate Europe, especially in the "deciduous forest belt" (fig 10, no. 1) . They are represented by a few species with a relatively wide distribution, for instance, *P. longifolia*, *P. angustifolia*, and *P. obscura*. In Siberia they are relieved by *P. dacica*, which area extends from North Yugoslavia to Rumania, Russia, East Siberia, and North China (fig. 1, 5) .

Other diploids are characterized by a more or less sporadic occurrence in the western and southern European Mountains, as well as in the Caucasus, in the Altai, and in the Tienschan (*P. angustifolia*, *P. visianii*, *P. carnica*, *P. rubra*, *P. filarszkyana*, *P. dacica* s. l.) .

The tetraploids are also characterized by restricted and scattered areas (*P. longifolia* pro pte., *P. montana*, *P. angustifolia* s. l., *P. kernerii*, *P. dacica*) ,

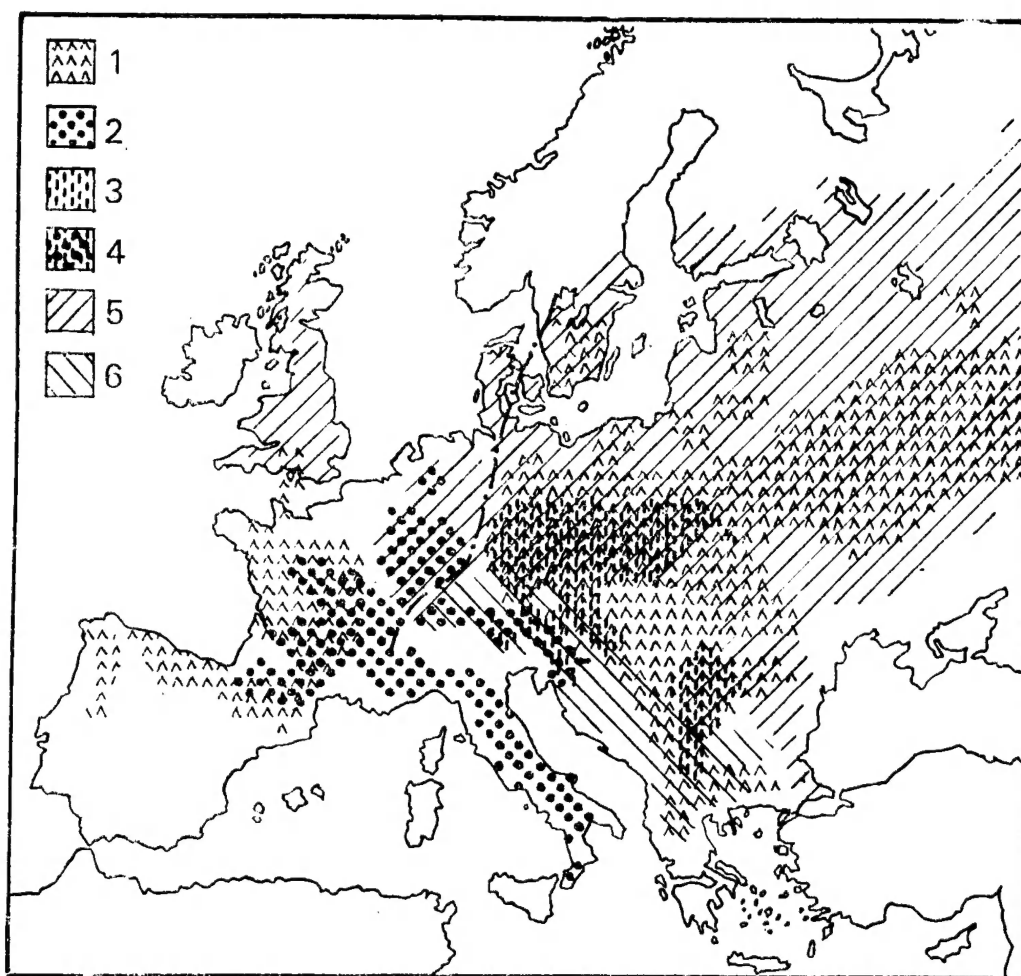


Fig. 10 Distribution of euploid and dysploid *Pulmonaria* species in Europe. 1 = Euploid species (2x, 4x), 2 = diploids of Southwest and South Europe, 3 = dysploids of East and Southeast Europe, 4 = overlapping of the areas of predominantly Southeast and Southwest European dysploid groups, 5 = *P. obscura*, 6 = *P. officinalis*. (According to Sauer 1975)

The dysploid species, however, are growing in widespread areas; they extend from upper colline to the montane and/or subalpine region. Principally they are found either in the west/ southwest or in the east and southeast of the Alps (*P. longifolia* pro pte., *P. affinis*, *P. helvetica*, *P. saccharata*, *P. australis*, *P. vallarsae*, *P. stiriaca*).

In the north of the Alps a clear border line between the atlantic-subatlantic and the Central European-sarmatic and South European diploids and dysploids could be detected (fig.10: dotted line).

This event might have taken place in context with the quarternary glaciation. At that time the Central European *Pulmonarias* may have survived in two refuge areas in Southwest and Southeast Europe, which areas have become important centers of diversification.

The progenitors of *P. obscura* probably already had been adapted

to a higher extent of continentality and thus they have been able to survive in the fringes of woodlands, which might have existed in the approaches of Pleistocene glaciers.

At that time, however, the closely related *P. officinalis* and its immediate progenitors might have grown in more favourable habitats of the southeastern periglacial part in Northeast Balkan Peninsula. Its occurrence (*P. officinalis*) in the Alps as well as the recent areas of other dysploids (i. e. *P. australis*, *P. saccharata* or *P. vallarsae*) indicate that in the Southern Alps during the Pleistocene no sharp differentiation has existed between the southwestern and southeastern species complexes.

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欧亚大陆北部管花植物系统发育模式的探讨

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摘要 本文通过形态学和解剖学的分析, 细胞遗传学(染色体特性的研究) 以及生态地理学的研究等间接方法探讨了紫草科Boraginaceae中肺草属*Pulmonaria*的发育模式, 推导了该属从晚更新世到现今的演化过程。

肺草属的分布区从伊比利亚半岛西北部延伸到东西伯利亚和中国北部, 从英国和斯堪的纳维亚南部分别延伸到希腊中部。

本属大多数现代种很可能源出于下列4个第三纪种群: *P. angustifolia*, *P. mollis*, *P. officinalis*, *P. rubra*, 它们通过广泛和重复的杂交而扩大了种群数目。从形态上看, 本属现有种类在叶形和毛被, 花冠内面的毛被等方面有所区别, 但不显著; 而花冠喉部毛环的存在则为本属的普遍现象。

本属染色体基数是 $\times = 7$, 所有种的染色体既有中部和亚中部着丝点的, 也有近端部着丝点的。有二倍体种, 也有四倍体种, 还有“非整倍体”的情况。同样是二倍体种, 但各种的组型不同, 比较组型的变异, 确定了它们的亲缘关系及地理起源。作者成功地分析了多倍体的胞核演变过程和非整倍体的生成机制, 提出了肺草属从二倍体水平向非整体到四倍体又至高级的非整倍体水平的系统演化模式(图9)。

作者认为: 在阿尔卑斯北部存在一条南北走向的界线(图10)。此线是肺草属二倍体与非整倍体的分界线。这一界线的出现与第四纪冰川有密切关系。在冰期西南欧和东南欧是肺草属两个重要的避难所, 目前已成为肺草属两个重要分化中心。

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